

Temporal and Spatial Recruitment Patterns in *Bankia martensi* Stempell (Bivalvia: Teredinidae)

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Abstract. Temporal and spatial variations in the recruitment of *Bankia martensi* Stempell, 1899 (Teredinidae: Bivalvia: Mollusca) were analysed in southern Chile.

B. martensi is the only species of shipworm inhabiting Chilean waters and the cause of severe damage to wooden structures in the sea. Two experiments were carried out over a period of approximately 20 years, in Codihué (41°54'S; 72°25'W) during 1979–1980 and Metri Bay (41°36'S; 72°42'W) during 2000–2001. Pine and oak panels were suspended at three depths and the density of recruits was determined based on the perforations or calcified cones produced when animals penetrate the wood.

Recruitment patterns were similar during both series of experiments. Average recruitment density did not differ statistically, neither did the incidence of attacks on pine and oak panels. Similarly, no differences were registered between the occurrence of attacks on the upper or underside of the panels. Seasonal differences did occur with regard to the period of maximum recruitment, although in both locations recruitment was significantly lower in winter. No differences were registered at depths of over 3 m, and lower recruitment was registered on superficial panels only in Codihué.

Results indicate continuous recruitment and low levels of temporal and spatial variability in spite of the different locations and periods when the data were collected. These patterns may be associated with the unpredictable presence of wood in the sea that is the specific substrate necessary for metamorphosis and adult development. *B. martensi* possesses reproductive characteristics that permit a constant supply of competent larvae, such as: reproduction throughout the year, early sexual maturity, alternative hermaphroditism and prolonged larval development, probably with teleplanic larvae. Low larval substrate selectivity also favours substrate colonization.

INTRODUCTION

There is only one species of wood-boring teredinid in Chile, *Bankia martensi* Stempell, 1899, which is the principal cause of attacks on wood in the sea (Stuardo et al., 1970; Campos & Ramorino, 1990). Recruitment occurs throughout the year (Campos & Ramorino, 1990), although factors operating at different spatial and temporal scales can generate variations in recruitment intensity. Antecedents do exist with regard to seasonal variations (Stuardo et al., 1970) as well as differential attacks according to the particular physical characteristics of different types of wood (Almuna et al., 1999).

Teleplanic larvae, common among teredinids (Scheltema, 1971), not only recruit on substrates at a distance from the breeders, but can also adjust their position in the water column in response to different environmental factors. In particular, reactions to light and depth are common in competent larvae of bivalve molluscs (Jackson, 1986). For this reason, the recruitment of *B. martensi* could vary seasonally according to the supply of larvae which is influenced by maturity periods and spawning factors, in addition to the degree of larval permanence and dispersion. It has been established that water circu-

lation patterns (Varotto y Barreto, 1998) and the physical effect of water conditions on larval mobility (Gara et al., 1997) can influence colonization in teredinids. Spatial variations in recruitment can be attributed to substrate characteristics and the position of larvae in the water column (Turner, 1984; Baker & Mann, 2003).

Recruitment of sessile or semi-sessile invertebrates can vary both spatially and temporally (Underwood & Keough, 2001), producing significant effects on populations. Recruitment variations may determine the number of individuals that reach maturity, since they affect the survival (Bertness, 1989). Recruitment variations can also determine the reproductive potential and functional condition of individuals that reach maturity (Sutherland, 1990). Evidence indicates that recruitment patterns account for fluctuations in population size throughout the year and between years, as well as the age structure of open populations (Roughgarden et al., 1985). Nevertheless, little is known about these aspects in teredinids.

This study aims to establish the recruitment patterns of the shipworm *Bankia martensi* by determining the effect of season, substrate location and type of wood in studies carried out during different periods and in different locations.

MATERIALS AND METHODS

Experiments were undertaken in two locations in southern Chile, with an interval of around 20 years between study periods. Experiments were initially carried out between October 1979 and October 1980 in the inlet of Codihué (41°45'S; 73°25'W) and then replicated in Metri Bay (41°36'S; 72°42'W) between November 2000 and November 2001. The sites are separated by a distance of 21.15 km, direct route. Both sites are located in the northern border of the Ancud Golf; Metri to the east of Reloncavi Bay and Codihué to the west. Oceanographic and climatic conditions are similar in both sites. Surface water temperature followed a clearly seasonal pattern in both locations, with average maximum tides of 7 m. Average monthly temperatures in Codihué ranged from 9.5°C to 16.8°C and in Metri Bay from 9.9°C to 17.5°C. Salinity in Codihué varied between 31‰ and 35‰ and in Metri Bay between 34‰ and 35‰.

Wood panels measuring approximately 20 × 10 × 5 cm were suspended from long lines at three depths: superficial, between 0.5 and 1 m; middle, between 3 and 4 m; and deep, between 6 and 8 m. Each group of 3 panels was placed at random, in triplicate. The panels were removed at monthly intervals and observed under a stereoscopic microscope in order to determine the number and density of recruits, based on the perforations or calcified cones produced when animals bore into the wood (Turner & Johnson, 1971).

Monthly registers for both locations and study periods were grouped seasonally, in order to establish temporal variability; spatial variability was determined by comparing recruitment at different depths on the upper and lower surface of each panel. Three-way variance analysis was used: season, depth and panel surface, following root transformation of data (Sokal & Rolph, 1969). The Tukey test was used for *a posteriori* analysis (Steel & Torrie, 1985).

Parallel to the above-mentioned experiments, degree of substrate selectivity was evaluated in both locations and study periods. For this purpose, panels of two types of wood were used: pine (*Pinus radiata*) and oak (*Nothofagus* sp.), and recruitment monitored over a two month

period. The wood was selected according to antecedents presented by Almuna et al. (1999), establishing that pine is more susceptible to attacks by *Bankia martensi* than oak. Data were compared with a two way and single variance analysis following root transformation. Similarly, we established whether recruitment was at random, using χ^2 according to Poisson.

RESULTS

Bankia martensi recruitment did not differ statistically either according to depth or between two closely located sites in southern Chile, where evaluations spanning a period of around 20 years were undertaken (Table 1); average density of recruits in Codihué during 1980, was $0.57 \pm \text{SE}: 0.09$ individuals·cm⁻² and in Metri during 2000, $0.69 \pm \text{SE}: 0.07$ individuals·cm⁻².

Recruit density on pine and oak panels did not differ either in Codihué ($F = 0.93$; $df = 1;42$; $P < 0.001$) or Metri ($F = 0.78$; $df = 1;11$; $P > 0.001$).

Spatial distribution of recruits on pine and oak panels submerged in Metri Bay was at random, following the Poisson rule ($\chi^2 = 14.38$; $df = 13$; $P > 0.05$).

B. martensi recruitment occurred throughout the year in both locations (Figure 1) and at all depths (Figure 2). Nevertheless, it was possible to differentiate periods of maximum recruitment. In Codihué (1980), highest levels were reached in spring/summer, with a drop in winter, when lowest recruitment levels were recorded ($F = 12.65$; $df = 3;29$; $P < 0.001$). In Metri Bay, on the other hand, highest recruitment occurred during summer/autumn, with significant differences compared to the winter period ($F = 14.5$; $df = 3;77$; $P < 0.001$).

Recruitment on the upper and lower surfaces of the panels did not vary, either in Codihué ($F = 0.29$; $df = 1;29$; $P = 0.10$) or in Metri ($F = 1.72$; $df = 1;77$; $P = 0.19$) (Figure 3).

Table 1

Two-way ANOVA of the number of *Bankia martensi* recruits in Codihué 1979–1980 and Metri Bay, 2000–2001, according to depth.

Source of variation	MS	df	F	P
Locality	0.006	1	0.46	0.49
Depth	0.026	2	1.98	0.14
Interaction	0.017	2	1.28	0.28
Error	0.013	84		

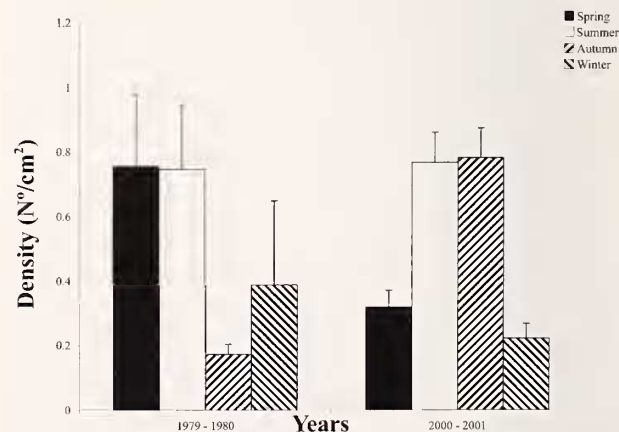


Figure 1. Average seasonal density \pm SE of *Bankia martensi* recruits in Codihué, 1979–1980 and Metri Bay, 2000–2001.

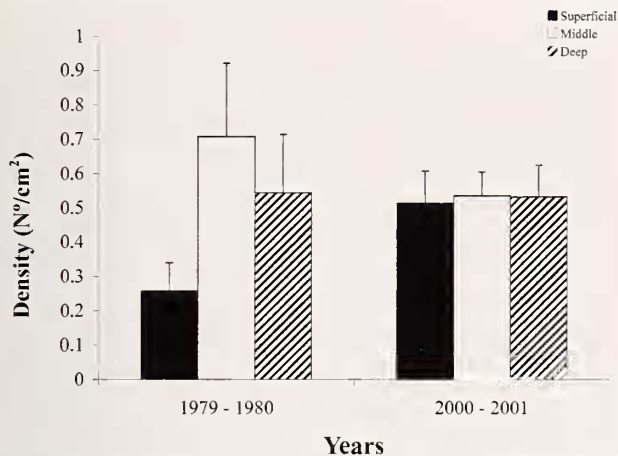


Figure 2. Average density \pm SE of *Bankia martensi* recruits at three depths, in Codihué, 1979–1980 and Metri Bay, 2000–2001.

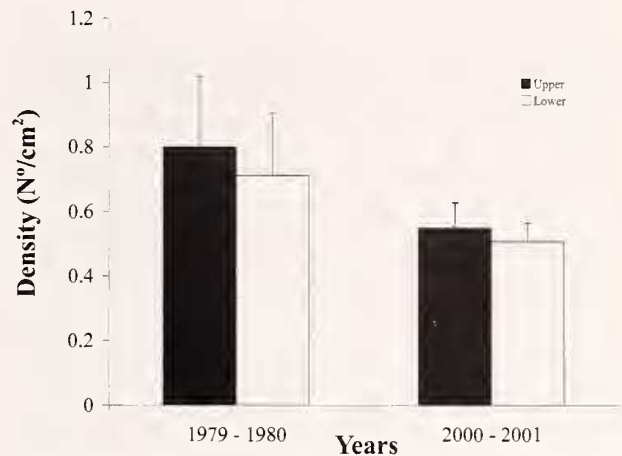


Figure 3. Average density \pm SE of *Bankia martensi* recruits on the upper and lower surface of panels, in Codihué, 1979–1980 and Metri Bay, 2000–2001.

DISCUSSION

Recruitment experiments were carried out on *Bankia martensi* in two sites in southern Chile, located close by, separated by an interval of around 20 years; results revealed low temporal variability. Recruitment occurred throughout the year in both locations, as recorded by Campos & Ramorino (1990), in studies undertaken in the area of Valparaíso, approximately 1000 km further north; this suggests that species reproduction-type is continuous, with successive gametogenic cycles during the year, which would account for the low degree of synchronisation between individual specimens.

Seasonal variations between study sites can produce local variations during periods of maximum recruitment. However, lowest recruitment levels always coincided with lower temperatures (winter). In studies carried out along the coast of Concepción, 600 km north of the sites being studied, Stuardo et al. (1970) recorded attacks on wood from the end of winter to the beginning of spring, suggesting that spawning would occur in spring and at the beginning of autumn. On occasions, *B. martensi* recruitment could occur considerably later than the spawning periods, since planktonic larvae may be highly dispersed, as generally occurs with veligers of the Teredinidae family (Scheltema, 1971). Thus competent larvae could colonize areas at a distance from the parental population. Furthermore, it has been established that recruitment and metamorphosis could be delayed in the absence of the substrate necessary for settlement (wood). Under laboratory conditions, pedivelifer larvae swam actively for more than 100 days after fertilisation when wood was not available and metamorphosised around 60 days after fertilisation in the presence of wood (Campos & Ramorino, 1990). Various morphological changes occur during metamorphosis; among others the disoconch develops initially along the anterior margin of the shell, creating a

denticulated external border which permits wood boring. If this does not occur, recruitment is not possible (Campos & Ramorino, 1990).

In *Bankia martensis*, as with other species of shipworm, a selective adjustment of reproductive processes can be expected in response to the availability of wood in the sea. Larvae only settle and grow on this particular type of substrate, whose temporal availability is estocastic. Thus, reproductive success should be substrate-dependent to a greater extent than in other species of sessile invertebrates. Reproductive processes should also tend to maximise colonisation of the substrate, both spatially and temporally. In the case of *Bankia martensis*, in addition to the capacity to recruit and grow on various types of wood, this is expressed in year-round recruitment and larval settlement with no significant spatial and temporal variations. These characteristics are the result of reproductive factors, such as early sexual maturity, successive gametogenic cycles, development of teleplanic larvae and hermaphroditism with autofertility, not necessarily protandric (Turner, 1973; Spormann, 2004).

Planktonic larvae of many species of bivalves can adjust their position in the water column in response to different factors, such as light, depth, temperature, salinity and current. This affects substrate colonisation (Jackson, 1986). The combined effect of light and pressure can determine variations in substrates located at different depths. Other factors such as the relative quantity of sediments and organic film on the upper and underside of substrates, could also cause recruitment levels to vary (Keough & Raimondi, 1995; Gara et al., 1997). In *Bankia martensis*, the only variations detected between study sites related to quantity of recruits on superficial panels. No variations were detected at greater depths, or between the different surfaces of the panels, confirming a low level of spatial variability in recruitment.

In *Bankia martensi* the presence of mature specimens all year round has been verified, including smaller sizes. Similarly, hermaphroditism, although non-protandric, has been confirmed (Spormann, 2004). Studies of sexual phases revealed that all the teredinid species are protandric hermaphrodites (Nair, 1962; Turner, 1966; McKoy, 1980; Hiroki et al., 1994). Hoagland (1978) has reported that due to the opportunist and sedentary nature of these species and the discontinuous availability of the substrate in the environment, they adopt protandry and minimise age of first reproduction, thus increasing reproductive potential. Nevertheless, non-protandric hermaphroditism is even more favourable to an opportunist strategy. Reproductive maturity in females is reached early. Campos & Ramorino (1990) have reported specimens with a shell length of 2.5 mm emitting gametes; this size is reached on wood panels maintained for 2.5 months in the water.

The larval development period in *B. martensi* plankton appears to be prolonged. Under laboratory conditions, wood boring starts 65 days after fertilization, and at 74 days larvae have already bored into the wood (Campos & Ramorino, 1990). The length of the development process is similar to that of other species of this genus such as *Bankia setacea* (Townsend et al., 1966). Although data obtained under controlled conditions cannot be extrapolated to the natural environment, they do suggest a high capacity for larval dispersion. The length of the larval period and current velocity determine the distance between recruits and parental population (Scheltema, 1971). The duration of the larval period has also been associated to population size (Jablonski, 1986) as well as to genetic continuity among populations (Scheltema, 1971).

All these reproductive characteristics tend to maximise colonisation on unpredictable substrates (Tuente et al., 2002), given that longevity depends on the size and perishable characteristics of the substrate where larvae recruit and grow. For this reason, difficulties have been encountered in controlling attacks on wood.

Efforts have been made to control shipworm wood attacks using chemical compounds that can operate at three levels: preventing larval settlement, increasing mortality prior to total settlement or provoking mortality after settlement (Giúdice, 1999). Copper compounds and organometallic compounds such as tributyltin fluoride (TBT), triphenyltin fluoride (TPTF) and tributyltin oxide (TBO) have been used in antifouling paints (Giúdice, 1999). However, antecedents indicate that they pollute the environment, in particular the latter compounds (Huggett et al., 1992). The need to settle on a specific type of substrate would limit the selectivity of competent larvae with respect to other substrate characteristics, as a result of which attacks on a wide variety of wood are to be expected. Although antecedents of differential attacks by teredinids do exist (Nair, 1962; Turner, 1984) including *B. martensi* (Stuardo et al., 1970; Almuna et al., 1999), it has been established that this species can attack all

types of wood, although with greater intensity on soft as opposed to hard woods (Stuardo et al., 1970). Nevertheless, a high degree of variability in attacks on panels of the same type of wood has been recorded (Stuardo et al., 1970; Almuna et al., 1999), which indicates estocastic processes associated with a complex group of factors that determine physical contact between larvae and substrates. Results obtained in the present study indicate that frequency of attacks on pine is similar to that of attacks on oak and that recruitment was at random.

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